

The natural diet of the endangered camaenid land snail *Thersites mitchellae* (Cox, 1864) in northern New South Wales, Australia

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ABSTRACT

The natural diet of the camaenid land snail *Thersites mitchellae* (Cox, 1864) was investigated by examination of the faecal contents of specimens collected from a range of substrates. The composition of faecal pellets from 22 snails obtained from three different substrates was determined. The results demonstrate that *T. mitchellae* has a generalist feeding strategy that varies with substrate. Fungal material contributed a high proportion of the diet, suggesting that coarse woody debris (a common fungal substrate) may be an important requirement for populations of *T. mitchellae* in rainforest-associated habitats. *Thersites mitchellae* was the first species for which a critical habitat determination was made under the New South Wales *Threatened Species Conservation Act 1995*. This study adds to our knowledge of the biology of this poorly known land snail. Future studies would benefit from obtaining data pertaining to the timing and frequency of fungal dispersal and substrate preferences to gain further understanding about the availability of fungi as a food source.

Key words: Mitchell's Rainforest Snail *Thersites mitchellae*, land snail, feeding, fungi, threatened species, conservation

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Introduction

Faecal analysis is acknowledged to be the most effective method of determining land snail feeding preferences under natural conditions (Mason 1970; Wolda *et al.* 1971; Richardson 1975; Speiser and Rowell-Rahier 1991; Mensink and Henry 2011). The technique is superior to direct observation of feeding behaviour, as it is difficult to distinguish visually between various snail activities (Ford and Cook 1994; Cook 2001). Furthermore, snails feeding in conspicuous places may be observed disproportionately more often than snails in cryptic habitats (Speiser 2001). Faecal analysis also provides dietary information without disturbing the snail's natural behaviour and habitat, and provides a quantitative measure of ingested food (Mensink and Henry 2011).

The vast majority of land snails are detritivores and many exhibit a generalist feeding strategy (Mensink and Henry 2011), consuming a variety of food including fungi (Wolda *et al.* 1971; Butler 1976; Ramsell and Paul 1990; Puslednik 2002), faeces (Bull *et al.* 1992), animal remains (Mason 1970; Wolda *et al.* 1971; Iglesias and Castillejo 1999), and soil (Williamson and Cameron 1976). Snail species occur in a wide range of habitats, and their diets differ according to location (e.g. Williamson and Cameron 1976; Iglesias and Castillejo 1999; Chang 1991). The quality and quantity of available food vary accordingly, as do the nutritional needs of the individual

(Speiser and Rowell-Rahier 1991). To date there has been little research into land snail food preferences undertaken in Australia (Parkyn & Newell 2013) despite the high diversity of species occurring here (Stanisic *et al.* 2010). Emphasis has been given to the study of introduced land snails (e.g. Pomeroy 1969; Butler 1976), but caution should be exercised in extrapolating what is known from European studies of species such as *Cepaea nemoralis* (Linnaeus, 1758) (Helicidae) and *Arianta arbustorum* (Linnaeus, 1758) (Helicidae) to Australian taxa. Puslednik (2002) demonstrated that two native Australian species of camaenid snails, *Meridolum gulosum* Gould, 1846 (Camaenidae) and *Meridolum* sp., showed a preference for fungi over plant tissue. It was suggested that further experimental work was needed to examine feeding preferences for these and other land snails.

Thersites mitchellae (Cox, 1864) (Camaenidae) is a regionally endemic Australian land snail that is found in lowland rainforest and swamp sclerophyll forest on coastal floodplain (Stanisic 1998; Murphy 2002). The species occurs in north-eastern New South Wales (NSW) and is listed as endangered under the NSW *Threatened Species Conservation Act 1995* (TSC Act), and critically endangered under the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act) (Threatened Species Scientific

Committee 2002). This was the first species for which a critical habitat determination was made under the TSC Act (NSW National Parks and Wildlife Service 2001a). Despite the conservation status of *T. mitchellae* many aspects of its ecology are unknown (NSW National Parks and Wildlife Service 2001b). The species is considered to be herbivorous and is thought to feed on leaf litter, fungi and lichens (Stanisic 2000). Snails are capable of relatively long-range movements within suitable habitat under favourable climatic conditions (Parkyn *et al.* 2014). Snails feed until their oesophagus is full (Speiser 2001), and it is assumed that food was obtained from discrete substrate types.

The natural diet of *T. mitchellae* was investigated by examination of faecal contents. Using an experimental approach, we explored how snail maturity (juvenile, adult) and the availability of food influenced the diet of foraging snails. The type and availability of macrofungi were surveyed at the site. The results of this survey and diet variability of *T. mitchellae* are presented.

Methods

Study site

The study site (28°40'S, 153°36'E) is located near Byron Bay in northern New South Wales, Australia (Figure 1). The site is a fragment of remnant and regrowth vegetation of approximately three hectares in size. The area is prone to frequent inundation, and is typical of coastal lowland habitat where *T. mitchellae* has been historically recorded (NSW National Parks and Wildlife Service 2001b).

described in Andrade *et al.* (2011). Eleven snails were captured and placed in separate containers until daylight. Captured snails were fed with saturated white paper shortly after midnight. The paper was used to encourage the passing of faecal material and to determine the lag time from feeding observations to defecation (Williamson and Cameron 1976). Strings of faecal pellets were expelled within 8 hours and were easily differentiated from the white paper waste. Pellets were preserved in 70% ethanol.

Once the preliminary tests were completed, an additional twenty-two snails were collected on 6 April 2011 by opportunistically sampling three different substrates (leaf litter, coarse woody debris [CWD], and rocks). Foraging snails were observed to minimise their movement in response to the abundance of food. The location of each snail was recorded using a GPS, and snails were captured and processed as previously described. The snails were classified as adult or juvenile by the absence or presence of an umbilicus respectively. Snails were returned to their original locations the following morning.

Faecal pellets collected from these 22 snails were stirred gently to produce slurry using approximately 5 mL of 70% ethanol. Slurry was extracted using a pipette and placed onto a microscope slide. Five slides were prepared for each sample. Two drops of 3% potassium hydroxide (KOH) were added to three of the slides to hydrate and clarify the ornamentation of the fungal hyphal walls (Assyov 2010). A drop of Melzer's Reagent (chloral hydrate 22 g, iodine 0.5 g, potassium iodide 1.5 g, distilled water 20 mL) was added to a fourth slide to assist with spore type identification. A drop of Congo Red (1 g of Congo Red in 99 cc water saturated in ammonium hydroxide) was added to the remaining slide to help visualise amorphous material without a cellular structure (Queensland Mycological Society 2008). Slides were covered with a 22 × 22 mm coverslip and sealed using DPX (Merck Millipore, UK). The stained microscopic preparations were used as a reference to assist in the identification of material found in unstained samples.

Faeces were viewed under a compound microscope (10×, 40×, and 60×), and the contents identified where possible and assigned to the categories: (i) plant tissue (mostly dead foliage, but also including some flower, root, or stem), (ii) fungi, (iii) soil material, and (iv) 'other' material. The percentage composition of the faecal contents was determined by estimating the percentage of each food item from five randomly selected fields of view of each of five slides for each snail faecal preparation (Figure 2).

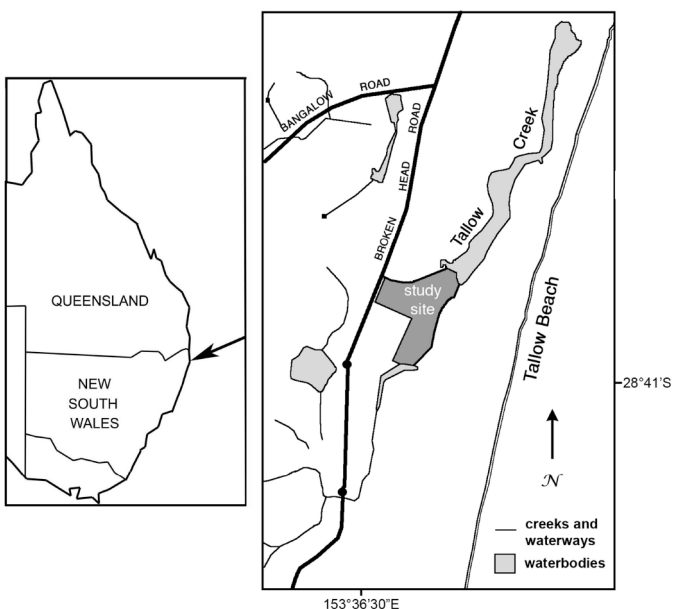


Figure 1. Location of study site in northern New South Wales, Australia.

Faecal analysis

A preliminary on-site survey was conducted on 26 February 2011 to assess the method of snail capture and collection of faecal material. Nocturnal observations of *T. mitchellae* were conducted for 5 hours (7 p.m. to midnight) during the hours of peak activity, following the method

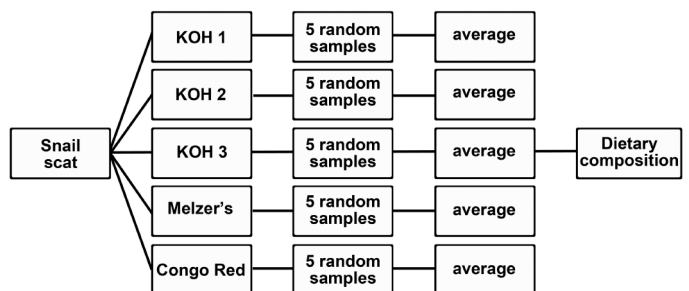


Figure 2: Schematic illustration of the procedures used to prepare microscope slides for faecal analysis.

Two-way analyses of variance were used to analyse the main effects and interaction of the maturity (juvenile, adult) of individual snails and substrate (leaf litter, CWD, rock) on the percentage of (a) plant, (b) fungal and (c) soil material in the diet. Non-significant interaction effects were removed from the model and a main effects model fitted. The models were fitted using the general linear model (GLM) univariate procedure in IBM SPSS V19.0 followed by Tukey's post hoc tests.

The same model fitting process was followed in each case, as follows:

Step 1. The full-factorial model was fitted:

$$Y_{\text{snail}} = \text{factor1}(\text{maturity}) + \text{factor2}(\text{substrate}) + \text{factor1} * \text{factor2} + \text{error}.$$

If the interaction effect was non-significant ($p \geq 0.05$), step 2a was followed. If the interaction effect was significant ($p \leq 0.05$), step 2b was followed.

Step 2a. Fit the main effects only model:

$$Y_{\text{snail}} = \text{factor1}(\text{maturity}) + \text{factor2}(\text{substrate}) + \text{error}.$$

Multiple comparison tests between levels of significant main effects were conducted:

If the maturity effect was found to be significant, adult and juvenile means were compared.

If the substrate effect was found to be significant, Bonferroni-adjusted tests were performed on the three comparisons: leaf litter v. CWD; leaf litter v. rock; CWD v. rock.

Step 2b. The interaction effect in terms of multiple comparison tests in two families was interpreted:

Family 1: in each substrate, adult v. juvenile

Family 2: in each maturity class, Bonferroni-adjusted tests of the three comparisons: leaf litter v. CWD; leaf litter v. rock; CWD v. rock.

Macrofungi

Opportunistic sampling of macrofungi was done by walking through the three hectare site, photographing and collecting conspicuous sporocarps. For most macrofungi collections photographs and spore prints were taken, and specimens were subsequently dried as voucher material for identification. Preliminary identifications used local field guides (Young 2000; Grey and Grey 2005; Fuhrer 2009). Identification of significant sporocarps was conducted by McMullan-Fisher from photographs.

Opportunistic sampling of macrofungi does not yield quantitative data, but due to the patchy occurrence of sporocarps, allows the potential macrofungi diversity at a site to be estimated (Mueller *et al.* 2004), and provided insight into the numbers of fungal species likely to be encountered by *T. mitchellae* at the site. It should be noted, however, that considerable hyphal material may also be acquired by grazing surfaces of leaf litter and biofilms on other surfaces.

Results

Faecal analysis

Items in the faeces were identified where possible

and placed into four broad categories including: (i) plants, (ii) fungi, (iii) soil material, and (iv) 'other' material. Only three categories were used for statistical analysis, however, as 'other' material was a minor component that contained parasites, phytoplankton, and unidentified material. The faeces of nine juvenile and 13 adult snails were assessed.

The main effect of substrate was significant for both plant material and fungi. The mean percentage of plant material was significantly greater for specimens collected in leaf litter than CWD ($p=0.007$), or rock ($p=0.000$) substrates. While the percentage plant material was greater for snails collected among CWD than rock, it was not statistically greater ($p=0.084$). The mean percentage of fungal material was statistically greater for snails found amongst CWD than for those collected in leaf litter ($p=0.018$), or rock ($p=0.004$) substrates. However, the percentage of fungal material among the faecal material was greater in snails found among leaf litter than rock, but this was not statistically significant ($p=1.000$). The interaction of snail maturity and substrate was significant ($F=25.9$, $p=0.004$) for soil material (Table 1).

The interactions between main effects in the soil material were significant. The mean percentage of soil in the faeces between adult and juvenile snails from the rock substrate was significantly greater in juvenile than adult snails ($p=0.000$), while it was not significant for those found in leaf litter ($p=0.131$) or CWD ($p=0.308$) substrates. The mean percentage of soil material in the faeces of juveniles was significantly greater than in adult snails between rock and leaf litter substrate ($p=0.000$) and between rock and CWD ($p=0.000$). While the mean percentage of soil material in faeces was greater for animals collected in leaf litter than CWD, the difference was not statistically significant ($p=0.251$). The mean percentage of soil material in adult faeces was significantly greater in those found among rock than leaf litter substrate ($p=0.000$) and between rock and CWD ($p=0.000$). While the mean percentage of soil material was greater in those collected from leaf litter than CWD it was not statistically different ($p=0.583$) (Figure 3).

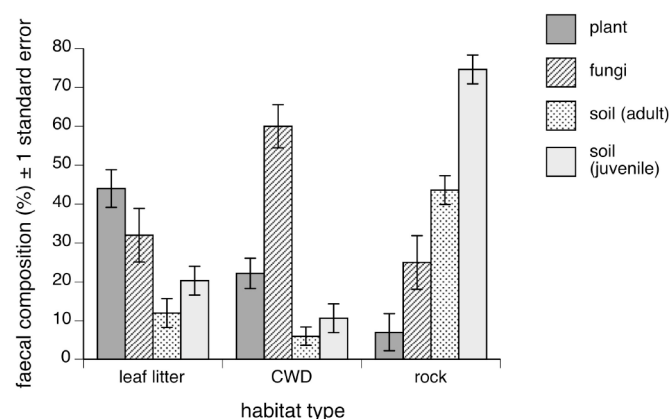


Figure 3: Mean percentages (± 1 standard error) for plant material, fungi, and soil found in scats for *T. mitchellae* in different substrates (leaf litter, 3 adults, 3 juveniles; CWD, 7 adults, 3 juveniles; rock, 3 adults, 3 juveniles).

Table 1. ANOVA tests of effects: F-values, degrees of freedom, and p-values from analysis of the main effects and interaction of snail maturity and substrate on the percentages of plant, fungi and soil in the diet.

Food		Effects		
		Adult/Juvenile	Substrate	Adult/Juvenile * Substrate
Plant (%)	F	0.547	14.876	0.582
	df	2,18	2,18	2,16
	n	13,9	22	
	p-value	0.469	0.000	0.570
Fungi (%)	F	2.205	8.778	1.017
	df	2,18	2,18	2,16
	n	13,9	22	
	p-value	0.155	0.002	0.384
Soil (%)	F	8.056	119.011	25.989
	df	2,16	2,16	2,16
	n	13,9	22	
	p-value	0.000	0.000	0.004

Note on p-values. Bolded values are from final models; non-bolded values are from initial (full-factorial) models.

Macrofungi

Thirty-one species of macrofungi from two Eucmycota phyla and one fungoid phyla (Myxomycota) were identified from opportunistic sampling across the site where snails were collected (Table 2 and Figure 4). Snails were observed feeding on several macrofungi species (Figure 5).

Discussion

Our results demonstrate that snails occupying different substrate tend to have different faecal composition. Our finding that the mean percentage of plant material in faeces was significantly greater for snails collected among

leaf litter than collected in other substrates is similar to that found in previous studies (Speiser 2001). In habitats where CWD was plentiful, the mean percentage of fungi in the faeces was statistically greater for snails collected from leaf litter or rock substrates. Furthermore, fungal material was a major component of the faeces for all snails. The preferential eating of fungi has been recorded for snails (Silliman and Newell 2003), and has previously been observed for camaenids in eastern Australia including *M. gulosum* and *Meridolum* sp. (Puslednik 2002). Snails are considered opportunistic fungivores (Trappe and Claridge 2005), meaning that they feed on fungi when they are available and in good condition. It is thought that the

Table 2. Phylum and taxa of macrofungi likely to be encountered by *T. mitchellae* at the site. Authority and family are shown for each. Species with an asterisk are shown in Figure 4.

Macrofungal taxa	Substrate		
	CWD	Leaf litter	Soil
Myxomycota			
<i>Ceratiomyxa fruticulosa</i> (O.F. Müll.) T. Macbr., 1899 (Ceratiomyxaceae)	×		
Ascomycota			
<i>Peziza</i> sp. ((L.) Dill. ex Fr 1822)) (Pezizaceae)		×	×
Basidiomycota			
<i>Auricularia</i> sp. (Bull. 1780) (Auriculariaceae), <i>Calocera</i> sp. ((Fr.) Fr. 1828) (Dacrymycetaceae), <i>Ganoderma</i> * sp. (P. Karst. 1881) (Ganodermataceae), <i>Hexagonia</i> sp. (Pollini 1816) (Polyporaceae), <i>Gymnopilus</i> sp.1 (P. Karst. 1879) (Cortinariaceae), <i>Gymnopilus</i> sp.2 <i>Microporus xanthopus</i> * ((Fr.) Kuntze 1898) (Polyporaceae), <i>Pleurotus</i> sp. ((Fr.) P. Kumm. 1871) (Pleurotaceae), <i>Polyporus</i> sp. (P. Micheli 1729) (Polyporaceae), <i>Postia</i> sp. (Fr. 1874) (Fomitopsidaceae), <i>Pycnoporus</i> * sp. (P. Karst. 1881) (Polyporaceae)	×		
<i>Crepidotus</i> * sp.1 ((Fr.) Staude 1857) (Inocybaceae), <i>Crepidotus</i> sp.2 <i>Cyptotrama asprata</i> * ((Berk.) Redhead & Ginns 1980) (Physalacriaceae), <i>Mycena chlorophos</i> ((Berk. & M.A. Curtis) Sacc. 1887) (Mycenaceae), <i>Pluteus</i> sp.1 (Fr. 1836) (Pluteaceae), <i>Pluteus</i> sp.2 <i>Pluteus</i> sp.3 <i>Polyporus arcularius</i> * (Batsch) Fr. 1821) (Polyporaceae)	×	×	
<i>Hygrocybe</i> sp. ((Fr.) P. Kumm. 1871) (Hygrophoraceae), <i>Mycena</i> sp.2 ((Pers.) Roussel 1806) (Mycenaceae), <i>Mycena</i> sp.3 <i>Mycena</i> sp.4 <i>Mycena</i> sp.5 <i>Mycena</i> sp.6 <i>Mycena</i> sp.7 <i>Psathyrella</i> sp. ((Fr.) Qué. 1872) (Psathyrellaceae)	×	×	×
<i>Cystoderma</i> sp. (Fayod 1889) (Agaricaceae), <i>Laccaria</i> sp. (Berk. & Broome, 1883)			×

snails seek out the fungi sporocarps by following the fungal odours (Kües and Navarro-González 2009).

For macrofungi to be available as large food resource they must be present as sporocarps. The production of sporocarps is weather dependent. There must be sufficient available water and suitable temperatures (Lodge *et al.* 2004). Subtropical forests with warm temperatures and plentiful precipitation often have conditions that favour sporocarp production (Fuhrer 2009; Mueller *et al.* 2004). Fungi are heterotrophs, thus must derive their nutrition in a number of ways: as decomposers (saprotrophs) of dead organic materials or as biotrophs: obtaining nutrients via either the parasitic consumption of carbohydrate from hosts (plants, animals and other fungi) or through mutualistic symbiosis as found in mycorrhiza and lichens (Dix and Webster 1995).

Previous studies have reported that soil consumption was significantly higher in juvenile than adult snails (e.g. Richardson 1975; Williamson and Cameron 1976; Mensink and Henry 2011). Our results indicate that juvenile *T. mitchellae* ingested a greater proportion of soil than adult snails on all substrates. Soil particles are regularly ingested by land snails in the natural environment (Williamson and Cameron 1976; Speiser and Rowell-Rahier 1991), but the role of soil in nutrition is not fully understood (Mensink and Henry 2011). It has been suggested that soil may aid digestion (Williamson and Cameron 1976; Hägele and Rahier 2001), supply nutrients (Elmslie 1998) or be ingested as a consequence of consuming soil organisms (Mensink and Henry 2011). The remains of animals are often detected in snail faeces, but apart from carnivorous snails (e.g. Stringer *et al.* 2003), this component constitutes a small fraction of ingested food (Mason 1970; Wolda *et al.* 1971; Speiser and Rowell-Rahier 1991; Iglesias and Castillejo

1999). Similarly, we recorded the remains of insects and nematode parasites. During our surveys we observed *T. mitchellae* feeding on a variety of food items including wallaby scats (Figure 5(E)) and bird-droppings.

A broad correlation between food availability and its proportion in land snail diet under natural conditions has been shown in previous studies (Speiser and Rowell-Rahier 1991; Iglesias and Castillejo 1999). Feeding accounts for a substantial proportion of snail activity (Cook 2001); as such their diurnal retreat site locations can have predictive value for food ingested on a previous night's excursion (Wolda *et al.* 1971). Further investigations on the proportions of time allocated to feeding, and retreat site selection within different habitats have identified small-scale feeding associated behaviour and substrate use of *T. mitchellae* (Parkyn *et al.* 2014). In general, the ability of the species to obtain energy and nutrients from a variety of food in different micro-habitats may account for its broad distribution at the site.

Sampling was also carried out to compile an inventory of macrofungi species present at the site. Most macrofungi of the thirty-one encountered during the survey have a decomposer life strategy. The exception is *Laccaria* sp. (Berk. & Broome 1883) (Hydnangiaceae), which is a *mycorrhizal* species obtaining its nutrition from plant partners. *Ceratiomyxa fruticulosa* (O.F. Müll.) T. Macbr., 1899 (Ceratiomyxaceae) may also absorb nutrients from living bacteria and protozoa as well as decomposing organic matter. Species of macrofungi have different substrate preferences (Boddy 2001, Jonsson *et al.* 2005), although there are some species that may be found across different substrates. Many of the taxa collected during the survey period were common on CWD (Table 2).

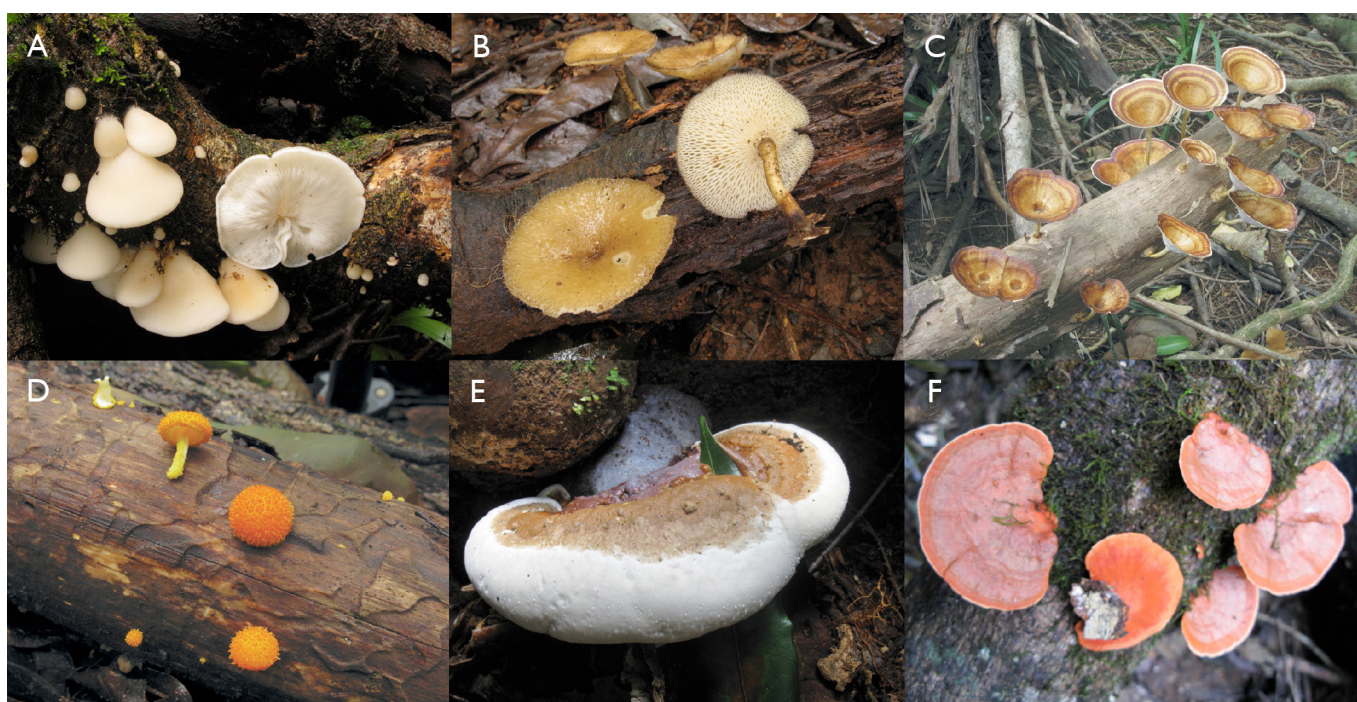


Figure 4: Some lignicolous macrofungi present at the site: *Crepidotus* sp. (A), *Polyporus arcularius* (B), *Microporus xanthopus* (C), *Cyptotrama asprata* (D), *Ganoderma steyaertanum* (E) and *Pycnoporus* sp. (F) (Photos: SJM McMullan-Fisher).

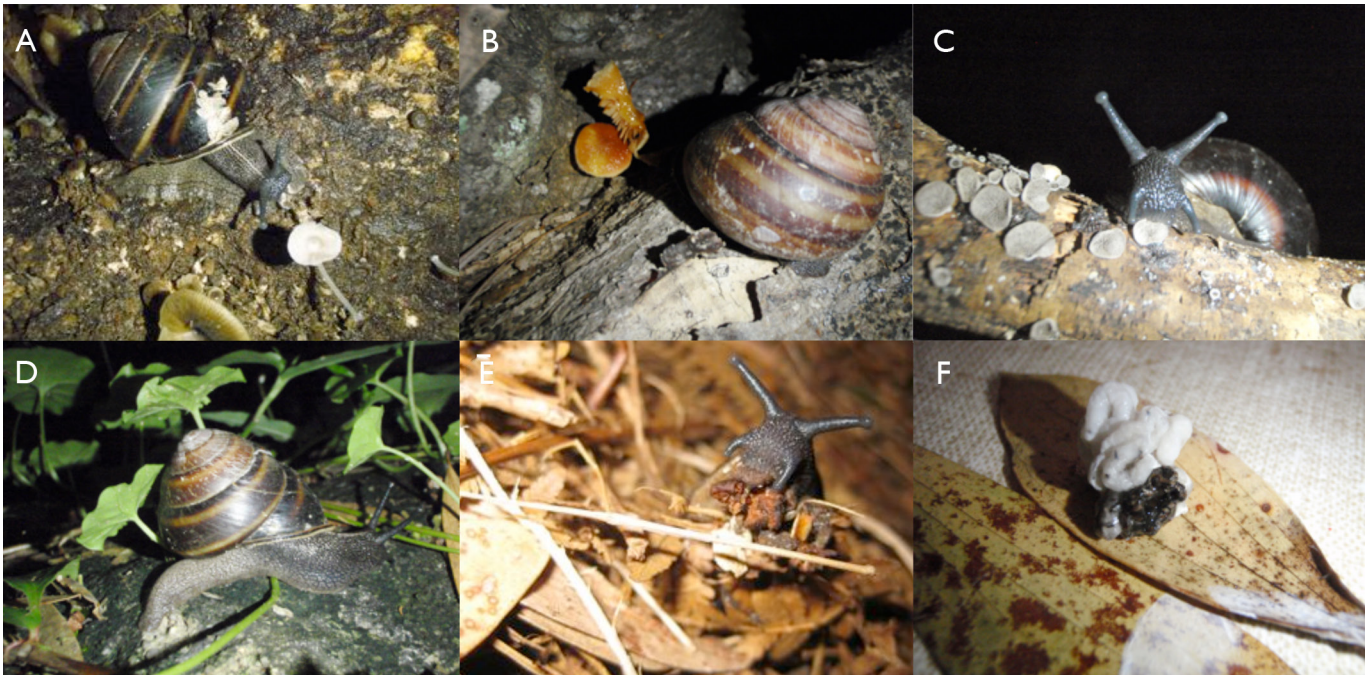


Figure 5: *Thersites mitchellae* feeding on (A) *Resupinatus* sp., (B) *Hygrocybe* sp. (C) *Mycena* sp. (D) lichen and bryophyte, (E) wallaby scat, and (F) String of faecal pellets next to white paper waste. (Photos: J Parkyn).

The higher percentage of fungal material compared with plant material found in the faeces of animals collected among rock has been interpreted as due to the presence of lichens. Fungi are heterotrophic and are unlikely to live on rock unless symbiotic partners or reasonable amounts of organic material are present; thus most fungi found on rocks are lichenised. Unless photobiotic partners (algae and cyanobacteria) are also found in scats it is not possible to tell the difference between macrofungi and lichen tissue. The lower percentage of fungi compared to plant found among the scats of snails collected from leaf litter may be due to there being fewer sporocarps on this substrate at the survey time. To understand further the availability of fungi as a food source, future studies to determine the timing of dispersal and substrate preferences of fungi would be beneficial.

Coarse woody debris was a common and productive substrate for macrofungi at the study site. Though many factors contribute to the distribution of the species at the site, the high percentage of fungi found in the faeces of snails in this study suggests that CWD may be an important requirement for populations of *T. mitchellae* in rainforest-associated habitats. These results indicate that a variety of fungi are readily ingested by *T. mitchellae* under natural conditions and influence micro-habitat selection, as such CWD may be considered as a key habitat component.

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